ART. IV.—THE ARCHITECTURE AND MECHANISM OF THE BRAIN.

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PRELIMINARY CONSIDERATIONS.

ALL higher manifestations of nerve force have for their organic substratum some one or several of the organs collectively designated as the central nervous system.

If we compare the mental manifestations in a given series of vertebrates on the one hand, and the development of this central nervous system in the same series on the other, we shall find that the higher the mental capacity, the more pronounced is the *differentiation* of the cerebro-spinal axis.

Again, if we trace out the successive evolution of the nervous system in the embryo, we find that the earlier embryos of lower and of higher animals are in this respect almost undistinguishable from each other, and that the human brain presents phases which in their serial succession closely simulate a series of adult brains of lower animals, arranged in their respective order of *complexity.*

Just as it is therefore evident that anatomically the substratum of the human mind has gradually developed from a condition far simpler than that of the brain as found in the adult, so may we infer that physiologically the highest nervous, that is the intellectual manifestations, are based in part on the unconscious registration of an immense phyllogenetic past, projected, as this is, in the anatomical perfection, produced *gradatim.*

The relations of the embryonic to the adult nervous system, in the light of this conclusion, assume a high degree of importance, and this importance is enhanced by the further and practical consideration that a knowledge of the embryonic nervous system bears to the knowledge of the adult nervous system the same relation which the study of the scaffolding of an edifice bears to a study of the edifice itself: it is an almost essential preliminary.

The cerebro-spinal axis of the adult presents us with such a maze of ganglia, such complicated topographical relations, and such a bewildering labyrinth of unilateral and commissural associating strands, and of direct as well as decussated and interrupted projecting tracts, that not only the student of general medicine, but even many of those who devote their attention to neurology, abandon the task of obtaining more than a knowledge of the cerebral outline as hopeless.

To lessen the labor of those who desire to understand at least so much of the cerebral architecture as is necessary for the comprehension of the cerebral mechanism, is the object of these lines. Following the architect's example, we shall endeavor to explain the human brain, by tracing its foundations as presented in the embryo and lower animals, and then following out the progressive building up of the elaborate superstructure which this organ presents in the human adult.

It is not proposed to furnish herewith a complete embryology or comparative anatomy of the brain, as little as it is our purpose to discuss histological and physiological questions *as such.* These pages, as indicated in their title, have no other unity in their plan than the accommodation of the physiological theory to the anatomical basis. Wherever the results of collateral science have appeared to us as calculated to assist in the clearer demonstration of the cerebro-spinal architecture, we have not hesitated to employ them. At the same time we have avoided these themes, where their introduction would have proved at best but a useless ballast.

§1. The characteristic attributes of every animated being are sensation and motion. Sensation consists in the molecular changes induced by outward influences acting on the animal; motion consists in other molecular changes which result in any alteration of the animal's position or form. In the simplest, as well as in the highest animals, motion is dependent on sensation; without sensation to guide it, motion would be an entirely useless property. It is evident that sensory influences must precede every *orderly* motor reaction!

Since both sensation and motion are ultimately reducible to molecular oscillations, the reaction of motion on the sensory influence must be considered as a transmission of molecular oscillations *from* the sensory *to* the motor end organs. Where the animal molecules are diffusely and homogeneously mingled, so that sensory and motor end organs are not differentiated, it

is easy to see that molecular oscillations must be transmitted from one to the other by the mere contiguity of the tissue molecules.

The course of progressive development is to make the animal as independent of its immediate surroundings as possible, that is, to increase its *freedom of choice.*

While the amœba will go on forever sending out its sarcode-processes and encircling floating objects, as soon as these come in contact with it, a higher animal will, under the same circumstances, have the choice of two alternatives—alternatives which the simple organization of the amœba is incapable of holding, the amœba being a blind slave to the immediate juxtaposition of its sensory and motor elements.

§ 2. The freedom of choice implies that the current passing from the sensory to the motor elements shall pass through an *intercalated medium.* This medium, which we will for the present *assume* to be capable of either *liberating* or *inhibiting currents*, is the nervous system.

§ 3. The nervous system follows in its structure the same plan exhibited in the bodily shape. It is built on the radiate plan in the echinodermata, it is distinctly segmental in the arthropoda, and in the vertebrata consists of an axial tube, which is also segmental, but less markedly so than in the arthropoda.

Let us take an ideal animal, and suppose it composed of a number of segments arranged end to end, giving it a worm-like shape. We will suppose each segment to be composed of sensory and motor elements, and a nervous system consisting of a simple arc, that is, a ganglion with an afferent fibre *from* the sensory, and an efferent fibre *to* the motor apparatus. If this were the sum total of the nervous system, each segment would appreciate sensation and enact movements entirely independent of the whole animal, and if impressions of different kinds were brought to bear on different segments, these segments would act so as to interfere with each other!

The organic necessity under which the animal is placed, demands harmony of action, and to produce this, it is necessary that the ganglia of different segments shall be in some sort of union. This union is effected by the *associating tracts.*

Through the tracts which connect the ganglion with the sensory and motor periphery of the same segment, the latter are projected in the ganglion; these are, therefore, its *projecting tracts.*

The basis of the most, as of the less complex nervous systems, is a series of ganglia, with projecting and associating fibres.

§4. As the extensity of a given force depends upon the mass of molecules, whose oscillation determines that force, it is clear that the larger the segment, in other words, the more developed its sensory and motor organs, the larger must be the ganglion of that segment.

From this fact we derive the first great law of the cerebral architecture, namely, *a ganglion (centre) follows in development the development of the periphery, which is projected in that ganglion.*

The lumbar enlargement is more marked in animals possessing powerful posterior extremities (man, kangaroo) than in those possessing weak or rudimentary ones (bat, porpoise). The cervical enlargement is proportionately larger in the bat, with its anterior extremities over-developed, and in the mole (for a similar reason), than in the dog and rabbit. The oculomotor and trochlearis nuclei are almost absent in the *pipistrella* bat, and entirely so in the mole, since the eyes of the former are poorly developed, and those of the latter rudimentary. The lower facial nucleus of the elephant follows the hypertrophy of the facial muscles (trunk); the hypoglossal nucleus in the seal is reduced, just as the tongue is limited in motion. The anterior tubercles of the corpora quadrigemina are atrophic in the bat and mole for the same reason assigned in the case of the oculo-motor nuclei; and in the land turtles the extreme atrophy of the parietal muscles in the dorsal region is accompanied by a greater diminution in the area of, and number of cells in the dorsal grey matter, than in any other animal. *Per contra*, in the axolotl and other urodela, as well as in the apodal lacertians (pseudopus) and snakes (anaconda, boa, rattlesnake), the cervical and lumbar enlargements are either scarcely, or not at all perceptible, just as the limbs are absent or insignificant.

§5. The ancestral vertebrate was a swimming animal, and its locomotion took place in the direction of the long axis. It was built upon the segmental type, and the nervous system may, for the clearer demonstration of what is to follow, be considered as composed merely of a series of segmental ganglia, and projecting as well as associating tracts, such as were mentioned above (§3). As the segments in this ideal pro-

genitor were originally all alike, the segmental ganglia must also be considered as alike, and none of them as preponderating over the other.

It alters nothing of this representation that even the simplest living vertebrates possess an unsegmented nervous tube. The ganglionic segments are to be considered as having fused typographically, while physiologically they have maintained their segmental distinctness. With all this, the nervous axis, even in high animals, exhibits a segmental *derivation*. In some fish (orthagoriscus, and our common gurnard) the spinal cord is composed of a series of enlargements, from each of which a pair of nerves arise; and all histologists must have remarked, in preparing sections from the human spinal cord, how a series of sections will be poor in ganglionic bodies, the next will be rich in these; again a barren field will follow, and so on in a quite regular alternation. The intervertebral ganglia, derived as they are from the medullary tube, maintain their segmental individuality throughout.

Now as this creature progressed through the water, the *anterior segments* were those which *first* encountered the foreign objects floating in the same medium; it was for these segments to determine whether these objects were inimical or indifferent or desirable to its individual ends! In the course of countless ages and through natural selection, the sensory periphery therefore underwent a high specialization *here*, certain of the end organs thus appear specially destined to appreciate the quality of the medium inhabited (olfactory), others to receive the rays of light, others certain oscillations of the surroundings (auditory), others finally, the strictly tactile organs, undergo an elaboration as such (tentacles, cirrhi).

But not only did certain special sense peripheries develop on the anterior or head segments, peculiar and important motor contrivances also became necessary. In the first place, since the head end was the first to encounter the prey to be captured or the enemy to be warded off, it was provided with powerful mandibular muscles, and muscles of deglutition.

Since in a water inhabitant, the respiratory medium was a fluid rushing in at the mouth, as the creature progressed through the water, the anterior or head part of the digestive tract underwent a modification resulting in the formation of gills at the very point where the respiratory medium was not rendered impure, as it would have been if it had had to pass through the whole length of the animal before becoming utilized. And since the object of the respiratory apparatus was

to bring the circulating fluids within the animal in contact with the gases contained in the respired medium, what more natural than that the circulatory centre, the heart,* should be also situated in the head end? The nearer the gills the heart, the less force is lost by the branchial blood-current.

Bearing in mind our first law announced, we perceive in this differentiation of the head *periphery*, the reason for the great development of the head *centre*. The eye, the *regio olfactoria*, the organ of Corti, the semi-circular canals, the gustatory papillæ, the muscles of deglutition, of ocular motion, of the maxillaries, as well as the great centres of circulation and respiration, are all concentrated on the first few segments of the body, and it is for the ganglia of these segments to increase correspondingly. Thus it is that the first ganglia preponderate over all the others as a *Brain*. And thus it is that the brain shows such complex relations in contrast with the relative uniformity found throughout the spinal cord.

§ 6. But it was not only the *ganglia* of olfaction, smell, taste, mastication, respiration and circulation that underwent such an increase in dimensions; superior as they were in functional importance to all the other ganglia, and exerting therefore a control over these others, it followed that the *associating tracts* joining the cerebral and spinal centres predominated over the associating tracts joining the spinal centres to their fellows.

The higher a brain in the scale, the more complex, the more voluminous also the tracts joining the brain and cord in functional union.

We have here a fundamental law of the cerebral mechanism: *The highest functions do not reside in any special centre, but in the functional union of several centres through associating tracts.*

Before adding further explanations of this law, and in order to understand its exact application, other features of the cerebro-spinal architecture dependent on its embryological development, must be understood as a preliminary.

It must not be forgotten that while the embryonic developments in their main features correspond to the ideal progression of the vertebrate series in

* In embryos and lower vertebrates the heart is in the cephalic and cervical regions.

evolution, that there are many modifications for special purposes, which forbid the regarding of the embryonic as an exact reproduction of the phyllogenetic development. On the other hand we should not fall into the error which has found an expression in many current works, that the development of nervous centres necessarily follows in the order of their functional rank. In a general way this is true, but a few months before birth the spinal cord is as far from perfection as several higher centres.

Embryological development, in short, follows phyllogenetic and physiological generalizations in their main features only, and is not an exact picture of either.

§ 7. Chemical analysis* shows that the ovum contains the same protein compounds which are characteristic of the nervous tissues. But while in the adult, these compounds are concentrated in certain depots and so disposed as to wield an orderly and methodic control over the other portions of the organism, they are in the ovum uniformly diffused throughout its substance.

§ 8. To this simple condition of the ovuline germ, there is an analogue in the lowest forms of the protozoa. The amœba is composed of as uniform a substance as the holoblastic egg, and just as each portion of the amœba is like to every other portion, so does each portion share all the functions of the entire animal. Any and every part of this simple creature is endowed with motion and sensation, besides the more purely vegetative functions.

Here evidently the nervous and non-nervous constituents must be chaotically intermingled, as compared with the degree of separation attained in higher animals.

From the optical and physiological similarity of the ovuline to the amœboid protoplasm we are justified in inferring that the former like the latter contains representatives of the nervous tissues, uniformly and diffusely distributed throughout its mass.

The correctness of this analogy is borne out by the fact that the impregnated as well as in a lesser degree the unimpregnated germs manifest *amœboid* movements. The germ of the trout, on account of its size and transparency, presents the finest illustration of these movements with which we are acquainted; it sends forth long processes, spreading out flat over the nutritive yolk, or collects itself into a spherical clump, all the while exhibiting flowing motions of its protoplasmic granules so distinct as to be visible even under a low power.

* Hoppe-Seyler, *Med.-Chemische Untersuchungen*, 1867.

§ 9. This crude condition of the germ merges into a higher one, even before the act of impregnation takes place. Preceding and accompanying this act, groupings of the finer and coarser grained protoplasms into separate formations have been observed* with other changes, which although they are not as yet susceptible of a clear interpretation, must be considered as preparatory stages of the more profound differentiation which inaugurates segmentation.

§ 10. Segmentation begins by the cleavage of the germ into two *unequal*† hemispheres. Both alike undergo repeated subdivisions until the well-known mulberry appearance ensues. It is noteworthy that the *larger* hemisphere which furnishes the substratum of the central nervous system (as we shall see) segments much more rapidly than the lesser. From this it naturally results that the derivatives from the larger hemisphere must spread out over and finally surround the derivatives of the other, and as these latter have by a central separation of their elements, become arranged like a sac around a cavity, and are in their turn lined without by the former, we have the *now vesicular* ovum composed of two concentric hollow spheres. These are known from their relative position as the ectoderm and the entoderm.

§ 11. The ectoderm, *chiefly devoted to the building up of the nervous system* and the organs of special sense, is derived from the larger hemisphere referred to above, and allusion has been made to the fact as being of some significance, that the primordial substratum of the nervous axis exhibits a far greater activity in the course of segmentation, than the substratum of most other organs. *It seems as if the higher functional potentiality of the nervous tissues were heralded in this more intense segmentative energy.*

§ 12. A portion of the vesicular ovum is remarked as being the seat of those changes which are most intimately related to the development of the embryo, it is therefore known as the *area embryonica;* within its limits the entoderm separates into two layers, of which the deepest is known as the hypoblast,

* By Eimer, Romiti, Ed. van Beneden, van Bambeke, Balbiani, Shenk, Törok, Goette, Hertwig and Fol.

† Ed. van Beneden.

and the other, nearer the surface, as the mesoblast. The latter is just beneath the ectoderm, which for purposes of nomenclatural uniformity we shall henceforth designate as the epiblast. There are therefore three strata in the *area*, which at first are mere membranous expansions, overlying each other; but soon a thickening occurs in the outer layer or epiblast, which forms the starting-point of the numerous and intricate changes culminating in the formation of the brain and cord.

§ 13. This thickening is in the axis of the future embryo, and is due to a local increase in size and number of the *epithelium-like* cells of the epiblast; it is the *primitive medullary lamina.* In obedience to certain laws of growth which it does not lie within our province to discuss here, this lamina becomes bent parallel to its long axis, like, to use a homely comparison, a long strip of tin would be rolled to form a gutter. The bending process is continued, so that the gutter becomes a pipe; in other words the lamina which was gradually transformed into the *medullary groove* is now a *medullary tube.*

Although embryologists have long corrected the old error that the *primitive streak* and *primitive groove* are the precursors of the medullary tube, yet several works on the central nervous system still cling to this erroneous and antiquated notion. This may serve to excuse a special reference to the fact (which reference ought to be superfluous) that the primitive groove or furrow is a temporary appearance, early and entirely obliterated, of no relation to the nervous system, and having a signification only for the zoologist, as demonstrating the existence of a *gastrula* stage in vertebrates.

§ 14. From the walls of this tube are developed the nervous tissues of the central nervous axis. The canal itself is the forerunner of the central canal of the spinal cord as well as of the *true* cerebral ventricles.

§ 15. It is by local differentiation, by preponderating growth of this, or atrophy of that part of the tube, by the mechanical influence of surrounding protective capsules, or the as yet undissolved connections with other embryonic structures, that the manifold differences of various sections of the cerebro-spinal axis are to be explained.

However complex the cerebrum, however numerous and apparently distinct from their surroundings the basilar ganglia and the nerve nuclei, however intricate the course of the nervous tracts of the isthmus in their primordial origin, they are

no more complex and no more differentiated than are the nervous elements of the cord. From the olfactory lobe to the conus terminalis all nervous tissue is originally represented by a simple *epithelial tube.*

§ 16. We have already (§ 4–5) in speaking of the ideal ancestral vertebrate referred to the close connection existing between the nerve centre and periphery of each animal segment. The same close connection is maintained in the embryo of the highest animals and this is the foundation of one of the most important modifications of the central nervous axis.

It is clear that the epiblast thickening when it becomes gradually indented and rolled into a tube, must retain its connection with the *parent epiblast* longest at its *dorsal aspect*, while the *ventral aspect* is driven down among the subdivisions of the *mesoblast.* Now as delicate fibrils begin to unite the medullary tube with the surrounding parts, and following the law of propinquity, connect each part of the medullary tube with those neighboring parts which are *nearest* to it, it results that the dorsal aspect is connected through the primitive nerve fibrils with the parent epiblast, the ventral (and lateral) aspect with the mesoblast. The epiblast develops the *sensory*, the mesoblast develops the *motor* end organs. Hence we have a fundamental differentiation of the nerve axis here, which is destined to influence the architecture of the brain and cord throughout life. *The dorsal (posterior) portion of the nervous axis is connected with sensory organs, the ventral (anterior and lateral) portion is connected with muscles.*

The accompanying diagrams (schematized from sections transverse to the axis of rabbit embryos of different stages) may serve to elucidate this relation. In all the epiblast is represented as composed of black quincunx spots, the mesoblast as striated, the hypoblast by open cubes.

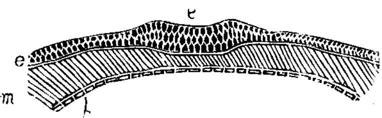


Fig. 1.

Figure 1 represents the earlier stage; here the three layers, epiblast, mesoblast, and hypoblast overlie each other as flat expansions; the epiblast (e) exhibits a medial thickening, the medullary lamina (é).

In a later stage (Fig. 2) the whole dorsal contour of the embryo becomes more convex; the medullary lamina becomes metamorphosed into the medullary groove (e); the dorsal aspect of the medullary groove can be seen to be continuous with the parent epiblast, and this is the future sensory seg-

ment of the medullary tube. The other or ventral part of the medullary lamina has moved to a position intermediate between the axial chorda and the protovertebræ (p), from which the voluntary muscles are derived.

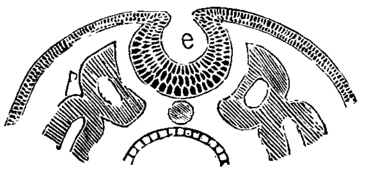


Fig. 2.

The mesoblast shows three primary subdivisions: one medial (the chorda) and two lateral parts. The lateral parts divide in turn into the protovertebræ (better termed segments, Götte, Entwicklûng der Unke) which lie nearest the medullary tube, and the lateral laminæ (segmental laminæ, Götte, *ibidem*). The cavity represented in the diagram as situated within the protovertebræ becomes obliterated; it is an isolated division of the slit observed between the inner and outer lamellæ of the lateral laminæ. This slit is the cœloma, or to use the more expressive polysyllable, the branchio-pleuro-pericardio-peritoneal cavity.

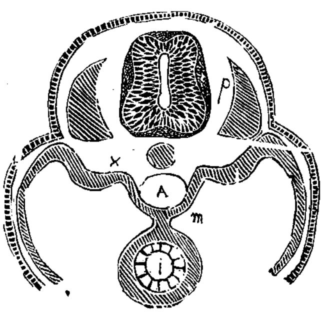


Fig. 3.

The lamella on its outer side does not interest us here; the lamella on the inner side, as shown in Fig. 3, forms the involuntary muscles of the aorta (A), thence the inner lamellæ of opposite sides join to form the mesentery (m) and then surround the hypoblast, which has closed to form the *enteric epithelial tube* as the muscular tunic of the viscera.

The cross-piece (x) uniting the outer and inner lamellæ, is the basis of the urogenital system.

Now it is easy to see that *from the beginning* the dorsal part of the medullary tube, when its fibrillæ sought peripheral connections (according to Hensen it is doubtful whether protoplasmic connections of the cells formed after segmentation are *ever* absent) must naturally have connected with the parent epiblast (Hornsinnesblatt), or the *sensory* and epithelial layer of the integument. And also that the ventral and lateral aspect must connect with the voluntary and involuntary motors. The subsequent union of the concentrated roots is a matter of purely mechanical moment, and does not alter this relation.

At the point where the parent epiblast was longest in connection with the medullary tube, the ganglia of the *posterior* roots (gasserian and intervertebral) are developed (these are not represented). It seems that cells analogous to those of these ganglia are *contained permanently within the nervous system, at two points where the mechanical factors which determine the separation of the intervertebral ganglia are absent or imperfectly exercised*, that is in the anterior segments of the medullary tube; to us it has always seemed as if the spherical nerve cells of the dorsal grey of the aqueduct and the cells of the *locus cœrulen* were of this kind.

It may be well to state here that originally the nerve roots are diffuse and

uniformly scattered around the periphery of the medullary tube, and that condensations at the root-zones occur only secondarily.

The fibrillæ which compose the future white covering of the cellular layer of the tube, show, according to Hensen,* three fundamental systems, a vertical and a radiatory, besides a circular. With advancing development the radiatory concentrates itself and develops at the expense of the longitudinal at the root-zones and raphes; the vertical develops at the expense of the radiatory *between* the root-zones, that is, in the white columns. The circular attains an important degree of development in the arciform fibres, the restiform decussation, trapezium and pons.

We have satisfied ourselves that this view of Hensen is correct, and agree with that author that the employment of the routine Canada balsam and damar mounting of specimens, renders many of the finer points in histogenesis invisible. But even in balsam specimens we have been able to see the multiplicity of the primitive rootlets (rabbit and batrachian embryos); hæmatoxylin specimens from chicks ranging from the fourth to the twelfth day of incubation finely show the gradual replacement of the uniform reticular arrangement of the fibrils, by the permanent fasciculi, at the expense of the outermost line of the proliferating cells of the tube.

It appears to us that just as the general differentiation of a motor and sensory district is explicable by the law of propinquity, that finer differentiations can be similarly traced, up to a certain point. The ventral muscles of the trunk and the flexors of the extremities would have their nuclei nearer the anterior commissure; those of the back and the extensors of the extremities nearer the so-called lateral cornu. Türck (Sitz, *Bericht der Wiener Akad.*, Band VI.) has proven a corresponding arrangement of the sensory provinces, referrable to the same embryological propinquity.

§ 17. As yet the medullary tube consists of nothing but more or less cubical and cylindrical cells, therefore we cannot speak of grey or of white substance: *both* are yet to be formed from these cells.

§ 18. Immediately surrounding the lumen of the medullary canal, the cells retain their epithelial character, and become in the adult the epithelium of the ventricular and spinal *ependymas.*

§ 19. Further outwards while the cells undergo proliferation, their protoplasm loses its contour; the cell bodies run together into a common mass, and the medullary tube exhibits the appearance of a uniform blastema, containing a large number of nuclei. These nuclei are the centres of formation for the *ganglionic bodies* commonly termed nerve cells.

§ 20. At the same time, the fused protoplasm of the cells develops delicate fibrils. These fibrils soon extend beyond

* Hensen, "Entwicklung des Kaninchens."

the limits of the cells, so that we now have an inner portion of the tube composed of the blastema and apparently free nuclei, and an outer composed of delicate fibrils which have developed from the blastema, and are more or less in connection with it. In very early embryos this fibrillary layer is an almost undemonstrable mere outer lining of the medullary tube, but it grows rapidly, and by subsequent nutritive changes, its fibrils become enveloped by myelin, giving it the characteristic appearance of *white* substance. Within the area of the nucleated blastema, there are also fibrils; but here they do not as a rule develop as differentiated a sheath as the fibrils in the white substance.

§ 21. Now the central nervous system contains two great categories of substances. The one which lies nearest the lumen of the medullary canal has been proven by experiment to be the seat of those molecular oscillations which determine the reception of impressions, and the motor reaction on these impressions. The substance of which it is composed usually exhibits itself in certain accumulations known as ganglia, for which reason we shall speak of it as *ganglionic substance.* It is indifferent for the first stages of this inquiry what the morphological arrangement of this ganglionic matter may be, whether it is arranged in cornua as in the cord, in nuclei as in the medulla, in scattered and diffused formations as in the entire isthmus, in large nodular accumulations, or surface expansions, as in the basi cerebral ganglia and the cortical grey substance; ganglionic matter has these fundamental physiological attributes, that it receives impressions and generates motor impulses.

§ 22. The second category is one without which the first, notwithstanding its high organization, would be a mere mass of functionless living matter. It has for its object the uniting of the ganglionic substance with the other tissues of the body. If this tissue is a sensory organ, it conveys the impressions received by this organ *to* the ganglionic substance; if this tissue is a muscle, it conveys motor impulses *from* the ganglionic substance to the muscle. In both instances it plays the rôle of a conductor; and, therefore, we speak of it as the *conducting substance.*

Anatomically, the ganglionic and conducting substances are not sharply demarcated. While those conducting strands, which for their more thorough isolation are provided with a myelin sheath, are grouped together in distinct fasciculi, the naked or grey fibres run directly into the grey substance. So that while the white substance is purely conducting, the grey is *both ganglionic and conducting.* In many localities even white fibres encroach on the ganglionic substance, as in the strands found in the fourth layer of the cerebral cortex, the white layer of the occipital cortex, and many other localities.

§ 23. It is an error to believe that the evolution of nerve force implies the existence of distinct fibres and of so-called nerve cells. Any protoplasmic accumulation of the chemical composition of ganglionic tissue, placed under the same influences as the latter is placed under in the living animal, is capable of developing nerve force. In the lower forms of animal life a uniform blastema with or without nuclei, and entirely devoid of nerve cells, is frequently all that represents a ganglion, and the afferent and efferent strands connected with such a simple structure are composed of an infinite number of granules which show no fibrillary arrangement.

Now as these lower animals are capable of performing comparatively complicated acts, and as the performance of complicated acts implies that the nerve machinery shall exhibit a certain constancy in its action, it is evident that there must be something in the *molecular arrangements* which forces the nerve currents to travel in given paths—paths which are defined and permanent, physiologically speaking, though undistinguishable to the anatomist!

§ 24. With the greater complexity of peripheral and intrinsic connections which the nerve axis presents in higher animals, the molecules begin to present that definite arrangement to the eye whose existence in lower animals was impalpable, except to physiological deduction. *The increased perfection of the nervous system is marked by a progressive tendency to isolation of the conducting strands.* We have the granules grouping themselves in granule-rows, or fibrils; and finally we have these fibrils surrounded by an isolating sheath.

At first in the embryo (§ 20) we have the conducting substance grouped in fibrils, which are connected with the periphery on the one hand, and terminate in the blastema, which

contains the nuclei of the originally distinct epithelia of the medullary tube, on the other.

§ 25. Radiating inwards through the substance of this tube, these fibrils make their way by creeping between, and meandering amongst, the free nuclei. At many points it can be clearly perceived that these fibrils form distinct groups around one or other of the free nuclei, and in doing so they include in their meshes a quantity of the blastema which surrounded the nucleus (Fig. 4). In this manner the ganglionic bodies are formed; a ganglionic body, therefore, consists of a nucleus, a certain amount of protoplasm around this nucleus, and of a greater or lesser number of fibrils which pass through, or at least penetrate into this protoplasm.

§ 26. The ganglionic corpuscle is hence a very complex body, and is not a cell in the proper sense of that term; but tradition has distinguished it as the *nerve* or *ganglion cell*, and as these terms will probably be adhered to in the English language to the end of time, we shall also use them, for the better comprehension of the reader, with the reservation mentioned.

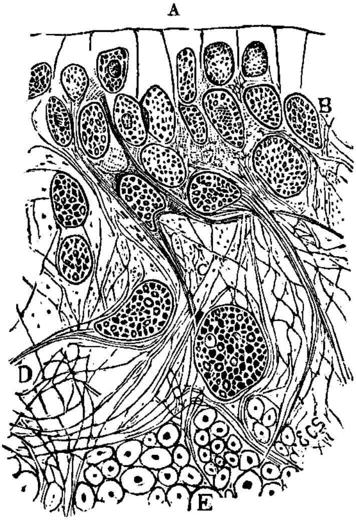


Fig. 4.

Section from the floor of the fourth ventricle at its posterior part (*menobranchus lateralis*, or American proteus); A, epithelium of ventricular floor, showing the large granular nuclei of the epithelia; B, nuclei, showing a

transition to the nuclei of nerve cells; C, fibrillæ, with scattered protoplasm; D, fibrils grouped into the process of a nerve cell, directed to raphe; E, white substance. × 350 diameters from author's specimen.

§ 27. From the fact that nerve cells are absent in very low animals, and that they become better and better developed and more and more numerous as we pass upward in the animal scale, but one inference can be drawn, namely, that *the nerve cell is the ultimate functional centre of the nervous system in man and other higher animals.*

It is necessary to insist on this fact, long ago accepted as a foregone conclusion, but recently attacked or questioned by some of our most eminent investigators. Some have claimed that the neuroglia is the real central field of nerve force, and that the nerve cell is merely a passage point for conducting fibrils, which are thus brought into a definite arrangement prior to their peripheral distribution. To this it can be answered that the neuroglia is relatively and absolutely present in greater quantity in lower animals than in man. And while we admit, and ourselves insist, that one object of the nerve cell is to bring numerous fibrils into definite groups, yet that this is not the only object of this elaborate body, is shown by the presence of a nucleus *unconnected* with the nerve fibrillæ, and of protoplasm scattered (however sparsely) among the fibrils. Nature has not placed these chemically highly complex bodies here without an object! The nerve cell is anatomically an elaboration out of the crude blastema, and just so physiologically its importance rises far above that of its mother bed, which latter in higher animals documents its waning physiological importance by simulating the character of a connective tissue. The neuroglia may hence be regarded as a part of the original simple ganglion, which retains its functional capacity in such a rudimentary form as practically to be of no importance in the mammalia, while the nerve cell is the part which usurped most of the functional material, and rose to the dignity of an individual centre.

§ 28. Careful anatomical research has shown that the nerve cell is provided on the one hand with peripheral connections, on the other with connections uniting it directly or indirectly with its fellows. Each single nerve cell exhibits therefore first ganglionic substance, second, connections *projecting* the motor or sensory periphery, and third, connections *associating* it with similar bodies. *The nerve cell is therefore a physiological unit, being provided with all the anatomical attributes which we predicated for the segmental ganglion* (§ 3).

§ 29. If we examine the nerve cells of a given cerebral ganglion, *known* to be the seat of a function or combination of functions which rises in extensity in the ascending animal

series, we shall find that the processes with which the cell is provided are few and simple in lower animals, and become more and more numerous as we pass up in the animal scale.

The cells in the anterior spinal cornu of the frog are very rich in processes, those of the salamander, and still more so those of the siren are therein poor; the spinal co-ordination of the frog is correspondingly higher than that of the urodela. The nerve cell of the cerebral cortex is a free nucleus in the menobranchus, bipolar in the amphiuma (Schmidt), has but few more processes in the scaly reptiles, fewer in the rabbit than in the dog, in the dog than in the ape, and in the ape than in man. (Herbert Major states in his paper on the cortex of a cynocephalus baboon, that he could discover no other difference between the nerve pyramids of the human and simian cortex than the lesser richness in processes of the latter. We can confirm this observation for macacus and cebus; in the chimpanzee we could discover no difference, taking into account that the staining was imperfect.) The proteus, amphiuma, reptile, rabbit, dog, ape and man occupy with regard to the respective number of processes appended to the cortical cell the *same* order which they occupy in the intellectual series!

Here we perceive that the nerve cell, following the law which we have announced for the *entire nervous system*, *gains in functional dignity with the increase of its associations.* We are justified in anticipating that where a given nerve centre varies in functional complexity in different animals, the cells composing it will show a parallel and related variation in the number of cell processes. The further inference will suggest itself to the reader, that where in a large series of animals, whether their motor co-ordinations be relatively sluggish or quick, whether their sensation be ready or obtuse, their intellect low or high, a given group of cells shows no variation in the number of its processes, that group of cells is not very likely to be in relation with voluntary motion or "conscious" sensation. By exclusion we should infer such a cell group to possess a trophic signification, for the trophic functions show the least variation in the animal range!

The application of this inference in the anatomy of the grey matter of the aqueduct and third ventricle will be discussed in its proper place. It is one of the numerous inferences which, theoretical as they are, constitute our sole guide in the obscurer fields of cerebral anatomy; their basis is highly logical, and although they may forever remain incapable of exact demonstration, yet all collateral facts are in their favor, while none can be urged against them. The trophic functions are more marked in the trigeminus than in any other cranial nerve, and this is the very nerve two of whose nuclei exhibit round cells similar to those of the intervertebral ganglia, and like these show no variation whatever in the entire mammalian series.

§ 30. The ganglion cells are all without exception at this early stage grouped around the lumen of the medullary canal. Consequently we have a continuous tubular cell column, extending from the anterior to the posterior extremity of the central nervous system, that is, from the anterior limits of the third ventricle to the filum terminale. The cerebro-spinal nerve fibres of the successive corporal segments terminate in topographically corresponding portions of this tube.

The primitive central nervous projection field for the peripheral end organs is therefore to be sought in the CENTRAL TUBULAR GREY MATTER, *that is in the grey matter of the spinal cord, the grey matter of the floor of the fourth ventricle, the grey matter surrounding the sylvian aqueduct and that lining the sides and floor of the third ventricle.*

Since the grey or ganglionic matter in which a spinal or a cranial nerve terminates, is often designated the nucleus of that nerve, the central tubular grey matter is also known as the *nuclear formation.* But not all so-called nuclei are equivalent to the central tubular grey matter in a strict sense: the term should be limited to the grey matter situated around the lumina mentioned, and not attached to the internodial nuclei of certain nerve strands.

The central tubular grey matter shows a tendency to nuclear differentation in all higher animals, and from this only such parts of the axis are exempt as have by becoming supplanted through secondarily established higher ganglionic depots, lost their functional importance. Thus the floor of the third ventricle over the chiasm, known as Meynert's basal optic ganglion, is the atrophic remnant of the primitive optic centre. From this point the pedicles of the ocular vesicle originated, and in the lowest fish the optic nerves terminate here (myxine). These relations will be discussed in their proper place, and their signification pointed out.

§ 31. The ganglia or nuclei of the central tubular grey matter are arranged in symmetrical groups. These groups on opposite sides of the median line are brought into functional association through fibres which cross the median line; this series of transverse fibres developed throughout the cerebro-spinal axis, constitutes the *transverse associating system of the primitive cerebro-spinal centres, i. e., those of the central grey.*

§ 32. The centres situated on different planes of the cerebro-spinal axis, but on the same side of the median line, are also

united with each other; those situated in immediate contact, by the fibrillæ of the grey substance itself, those situated at greater distances are connected by fibres which leave one centre to run through the white substance longitudinally, and enter the other lower or higher centre associated by its means. This is the *longitudinal associating system of the primitive cerebro-spinal centres.*

§ 33. The nervous system which we are now constructing, thus far consists of (a) a bilateral series of segmental nuclei, constituting the central tubular grey matter; (b) of projecting fibres connecting these nuclei with the sensory and motor periphery, known as the peripheral nerves; (c) of transverse associating fibres uniting the bilateral nuclei of the same segment; (d) of longitudinal strands of lesser and greater length uniting variously distant nuclei of different segments, but of the same side.

§ 34. In accordance with the principles enunciated in paragraphs five and six, the segmental ganglia of the head segments undergo a more massive development, and owing to their greater complexity of function develop more powerful association strands than those of the spinal region. Leaving out of consideration for the present everything beyond the third ventricle, we find that the *medulla oblongata* constitutes a hypertrophied segment of the spinal cord, and that the longitudinal associating fibres outweigh in *number* and *length* those of any other spinal segment.

The experiments of physiologists have shown,* that if a sensory irritation of a given spinal nucleus is kept up after having produced a reflex movement in the same segment, if there is any reaction beyond the plane of that segment at all, it is not in the next or succeeding planes, but in the *medulla oblongata.* The motor reaction then manifests itself in laughing, crying or deglutitory spasms, and if the irritation is of the severest kind, epileptic or tetanic spasms in addition.

Now the occurrence of laughing, crying or deglutitory spasms could be easily understood if we imagined the molecular oscillation induced by the irritation to travel along the associating

* Pflüger, "Ueber die sensorischen Functionen des Ruckenmarks." Berlin, 1853.

tracts from the given spinal segment to the nuclei of the medulla oblongata. For in the medulla we have the nerve nuclei that preside over the facial, laryngeal and pharyngeal muscles. It is not so easy to understand how tetanus and epilepsy, that is spasms consisting in movements whose *direct* projection is *not* in the medulla oblongata, but in the cord, are produced by irritation of the former.

There are scattered groups of nerve-cells in the medulla oblongata, which have mostly either no demonstrable connection with the nerve nuclei, or are positively known to be connected with the longitudinal associating strands. By logical exclusion we are more than justified in considering these cells as representing a presiding centre over the entire spinal system. No spinal centre exerts any influence even remotely as pronounced as that of the medulla oblongata on the *entire* cord.

This applies to man and the mammalia; that the elaboration of the medullary centre was as gradual a process as that of other higher differentiations is illustrated by the case of the frog, where the medulla has acquired the faculty of producing general spasms (it does not according to our experience possess this power in the perennibranchiate urodela) while the cord itself retains this property also, hence here the predominance of the medulla is not as marked as in the mammalia.

That the medulla relatively and secondarily loses in importance in the highest mammals alters nothing of the conclusions of this paragraph, as will be shown.

§ 35. If distal as well as direct irritation of the medulla can equally produce spasms of all the muscles (voluntary and vasomotor) of the body, and if sensory irritation of *any* part of the trunk and extremities can provoke the spasms originating in the medulla, it necessarily follows that all *the sensory and motor end organs projected in the grey matter of the spinal cord must be also projected in the reticular ganglion of the medulla oblongata.* This projection is not an immediate projection such as that established by the termination of the peripheral nerves in the central tubular grey matter, but mediate *through* the central tubular grey.

Accordingly this projection takes place through three elements which are arranged in anatomical and physiological continuity. At one end we have the periphery, at the other the reticular ganglion of the medulla; the connection is estab-

lished by (a), the spinal nerves, (b) the central tubular grey matter, and (c) the longitudinal associating tracts joining the spinal and medullary grey.

Reticular Ganglion
of
Medulla Oblongata.

Strand uniting Reticular Ganglion and
Central tubular grey.

Central tubular grey.

Peripheral nerve.

Periphery.

Here the ASSOCIATING *fasciculus becomes a part of the* PROJECTING *system.*

§ 36. We have stated (30) that the primitive projection field for the peripheral end organs is the central tubular grey matter, and that the primitive projection takes place through the peripheral nerves. To systematize our explanation of the cerebral architecture, we shall distinguish the central tubular grey matter as the *first* GANGLIONIC CATEGORY, the peripheral nerves as the *first* PROJECTION TRACT, both together constitute a *projection system of the first order.*

The reticular ganglion of the oblongata is not in the adult a part of the central tubular grey matter, but has, though originally developing from it in the embryo become ultimately isolated from its mother bed. It constitutes a *second ganglionic category*, and the association fibres bringing it in functional union with the spinal grey (first category) in lower animals, and shown to have assumed the position of projection fibres in the higher, constitute a *second projection tract;* both together are a second projection system.

The first projection system is perfect in itself, as far as it

goes; the second is a supplanted system, and would be imperfect if it did not, so to speak, stand on the shoulders of the first.

Our classification differs from that proposed by Meynert ("Beiträge zur Kenntniss der centralen Projection der Sinnesoberflächen," 1869; Stricker, *Gewebelehre*, II., on the brain of the mammalia). This author, the founder of the projection theory, and as yet the only one who has ventured with any degree of accompanying success to bring cerebral physiology to an anatomical basis, speaks of the central tubular grey as the third category, the great ganglia as the second, and the cortex as the first.

We hold that just as the physiologist must study the reflex processes before studying the automatic and psychical ones, so the lowest and reflex centres must take precedence of the higher in the anatomical delineation. The central tubular grey is the *first* formed, and in the amphioxus is the *only* category of grey matter in the central nervous system. Now assuredly it would be very confusing to the student to speak of the third category in the embryo and the amphioxus when a first and second category are in the former not yet isolated and in the latter permanently absent.

We also differ from that ingenious author in erecting a special category for the accommodation of the *reticular ganglion*. To our knowledge no author has yet given a name to the scattered grey matter of the medulla oblongata, although it has been very accurately described by Clarke, Dean, Meynert, Stilling and others. Its importance inferentially is great, and anatomically it is (though its cells are scattered diffusely *as a rule*) a large ganglion with numerous multipolar cells of all sizes, many of them are of gigantic dimensions and sometimes exceed the so-called motor cells (which they simulate in shape) of the lumbar enlargement in size. Scattered in the "reticular substance" of the medulla from the upper end of the fourth ventricle to the pyramidal decussation they merit the collective designation of a *reticular ganglion*, as we shall develop further on.

While we follow in the main the principles maintained by Meynert, we offer a different classification, one which has physiology, embryology and comparative anatomy in its favor. It remains for the reader to decide whether it possesses the same degree of clearness which attaches to Meynert's excellent plan. Meynert made but three categories (exclusive of the cerebellar grey), we see ourselves compelled to make more, thinking our system to necessitate less bold theorization and generalization, while it is more in accord with anatomy than the *schema* of Meynert. Wundt (*Psychologische Physiologie*) has already pointed out one grave inconsistency of Meynert's in regard to the nucleus dentatus (seq.), and there are other impeachable points in the system. This alters nothing of the fact that Meynert is the pioneer of *applied* cerebral anatomy, and this may be a proper place to dispose of some objections made against his projection theory.

Thus Flechsig ventures to question the greater part of Meynert's deductions on the strength of the fœtal development of the medullary strands. While we owe several valuable facts to this author, yet his results as a whole show very little of the positive beyond what had been discovered on pathological and physiological or anatomical grounds, by Türck, Stilling, Schief-

ferdecker and Meynert. His method has been over-rated, and such results as his methods have enabled him to obtain in the medulla must yet pass in review before competent anatomical critics. Such grave errors as the confounding of the acoustic nerve root with the inner division of the lower cerebellar peduncle render the value of these results quite problematical.

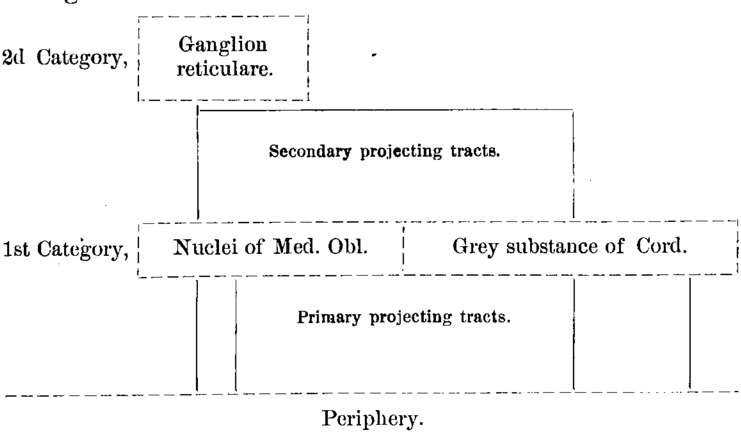
Flechsig's dictum that the nerve fibres of a given system become provided with myelin *throughout at about the same time*, is an error, for the *processus e cerebello ad cerebrum* becomes white much later in the supra-tegmental than in the infra-tegmental portion. And as if to show beyond any possible doubt that Flechsig's theory stands on very weak grounds, Rohon (*Untersuchungen uber den Bau eines Microcephalen-Hirnes*) has shown that the spinal fibres and those of the motor decussation were fairly developed in a monstrosity which had not even a trace of the pyramids above the decussation, the entire cerebrum not being larger than a chestnut. Thus showing that fibres unquestionably normally connected with a given centre, are not always dependent in their embryonic development on that centre, and on the other hand demonstrating that a fasciculus does not develop in all its length progressively or simultaneously.

The objections of Forel are based on much safer grounds, and this writer, who if he errs at all, errs on the commendable side of excessive caution, has made several corrections of Meynert's theorem, which are now to be accepted as final (see relations of Corpora Quadrigemina, Corpus Geniculatum Externum, Corpus Luysii, Fasciculus longitudinales post. Tegmenti). They have, we hear, been accepted by Meynert himself, at least in part.

But in his valuable and exhaustive monograph on the tegmentum (*Archiv fuer Psychiatrie*, VII.) he makes certain demands upon the cerebral anatomist who would offer an anatomical basis for the physiological theory, which can never be realized. He insists that the fibres of a fasciculus must be traced to a ganglion with which it seems to be connected, before that ganglion and fasciculus can be ranged in a system. Now this is but rarely possible even with the nerve roots, and to insist on this point would simply be a bar to cerebral anatomy. No one has yet seen a single fibre of the optic nerves enter the cells of the optic lobes, and yet no one can doubt that they do so from the concurrent testimony of comparative anatomy and physiology! No one has ultimately traced the hypoglossal fibres in any one section to the hemispheres, and yet we know almost their exact course from pathological experience! There can be no doubt of the relation between the olivary body and the cerebellum, and yet no one has seen the fibres ever connect with the cells of that body! True, many of Meynert's deductions were purely hypothetical, and it would have been well if that author had not through his categorical style given the impression that he presented as facts what were merely ingenious deductions *founded* on facts. But he is not open to the charge which Forel makes (from a strange misunderstanding), that he claimed to trace the fibres of all the projection systems in longitudinal sections of the brain. He traced whole *fasciculi* thus, and was justified in so doing, not individual *fibres*. As no fibre runs the length of the brain without repeatedly changing its course, no single fibre can be traced any considerable distance. But a fasciculus can usually be safely traced, unless,

like certain spinal bundles, it exhibits the *false appearance* of a compact bundle by gradually replacing fibres which it loses on one side by receiving fibres on the other.

§ 37. It follows from the preceding (§ 34, 36) that the medulla oblongata contains *both* the enumerated projecting systems, for we have the cranial nerves representing a first projection tract, their nuclei a first ganglionic category (the original central tubular grey), while the reticular ganglion represents the second ganglionic category. Now just as the second system is superimposed on the first system of the spinal cord, it is superimposed on the first system of the medulla oblongata, and this through fasciculi joining *some* of the cells of the reticular ganglion to the cranial nerve nuclei. These fibres represent the secondary projecting tracts. The projecting systems, so far as traced, present the following arrangement:



Wherever the cerebral anatomist encounters a large cell group, his first question is as to its connection with neighboring fasciculi. If these are known the function of the cell group can usually be deduced. The cells of the reticular formation are *known* to be connected with the nerve nuclei on the one hand, and with longitudinal fasciculi, which since they run into the cord, we infer to terminate either in the grey matter (or the nerve roots directly), for nerve fibres do not terminate with, as it were, blind ends. Now in the *mammalian* brain the reticular ganglion lies scattered among fibres which come from higher centres, and the interpellation might be made whether, after all, the reticular ganglion is not a mere intercalar station for fibres derived from a higher source. That *originally* the ganglion was an independent station, it can be answered, there is no reasonable doubt, for in reptiles this body of cells is too considerable to account for a

termination in them of the *few* cerebral fibres possessed by these animals. And, on the other hand, the vertical strands are notably increased in their passage through the field of the medulla oblongata.

The medulla oblongata, with its reticular ganglion, seems to be the great rhythmical centre. In fish, the movements of the operculum and mouth; in sharks, those of the spiraculum; in perennibranchiate amphibians, the branchial tree; in the infant, the suctorial muscles; in all vertebrates, the movements of deglutition, of the heart and the respiratory muscles; *all* movements presenting a more or less regular *rhythm* are under the control of the medulla oblongata.

The early differentiation of this part of the cerebro-spinal axis is, without doubt, related to the early manifestation of rhythmical movements in the embryo, and their predominant importance in lower animals. Not that we intend to exclude the possibility of a rhythmic movement being purely spinal, nay, even controlled by *peripheral* ganglia (heart of embryo), but that a higher development implies the concentration of rhythmic innervations at some point where that anatomical association may be effected, which is the expression of the mutual influence which these movements exercise amongst themselves. (Seq.)

§ 38. The scattered ganglionic matter of the medulla oblongata, although not a part of the central tubular grey in the adult, is *derived* from it in the embryo. All through the primitive medullary canal we observe a tendency for the central tubular grey to send out peninsular processes, and to scatter its cells through the contiguous white substance. The peninsular processes are usually drawn out in the direction of the nerve roots to form the cornua in the cord, and the nerve nuclei in the medulla oblongata. The scattered cells in the cord become indifferent bodies and atrophy, or are utilized in the formation of the connective substances; but in the medulla oblongata they form accumulations crowded away from the nerve nuclei by white substance, and thus form the reticular ganglion.

Anterior to the proper field of the medulla oblongata, similar scattered cells form the basis of the intercalar ganglia—which we shall speak of later on—and further forward on the sides of the third ventricle they form a massive accumulation —the *thalamus*. We shall, for the better comprehension of the relations of this body, be again compelled to refer to the embryonic development of the brain.

§ 39. The first indication of the cerebral formation is a pyriform enlargement of the anterior end of the medullary

tube. This enlargement is like the parent tube—hollow. The walls of the enlargement (*primitive cerebral vesicle*) are composed of the same elements, arranged in the same radiatory manner as the walls of the rest of the medullary tube. Through all subsequent morphological changes, the cellular elements of the brain hence maintain a vertical position to the surface contour of their respective locality, unless their position is disturbed by interrupting fibres.

§ 40. The primitive cerebral vesicle exhibits two constrictions, which subdivide it into three lesser segments, each of which contains a more or less round cavity, connected with the other cavities by the constricted lumina. These vesicles we designate as the (1) *fore-brain* (prosencephalon); (2) *mid-brain* (mesencephalon); and (3) *hind-brain* (prosthencephalon).

§ 41. The fore-brain undergoes a subdivision in the median line (median longitudinal fissure), which division does not extend all the way, however, but leaves the posterior part of the fore-brain untouched. This latter portion constitutes, according to anatomists, a separate division of the fore-brain, and is known as the *thalamus* (thalamencephalon). In the embryo, as well as in the adult, in the lowest, as well as in the highest animals, the thalamus maintains both a direct anatomical continuity and close physiological relation with the anterior segment of the prosencephalon, which, split in two by the posterior longitudinal fissure, we designate as the *cerebral hemispheres.*

From the fact, to be developed later on, that the thalamus and hemispheres constitute a structural continuity, and exhibit a mutual dependency of the closest kind, we refuse to accept the fundamental distinction made by comparative anatomists (untenable as it is even on comparative anatomical grounds), and range the thalamus as a ganglion of the hemispheres side by side with the corpus striatum.

In the reptiles and amphibians this relation is manifested by the direct continuity of the cortical cells with those of the thalamus at the base of the fore-brain. In menobranchus (Fig. 5) the thalamus constitutes a hardly perceptible enlargement of the central tubular grey, continuous with the similar more external enlargement of the corpus striatum, and where this is absent, with the cortical grey directly. In the alligator a special ganglionic hypertrophy of the thalamus is induced by the termination in it of that

part of the hemispheric inflection which corresponds to the cornu ammonis, a relation which is but slightly modified in the lower mammalia (Fig. 7).

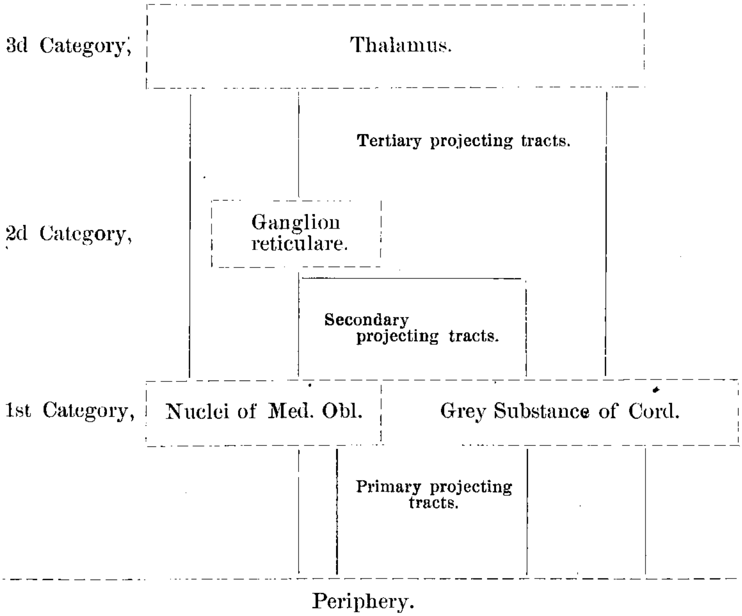
This is also, perhaps, the best place to briefly refer to the embryonic segments of the cerebral vesicle. It is ordinarily taught that after a certain stage, in which only three vesicles, as mentioned in the text (§ 40), are present, that by further subdivision these form six secondary divisions (German authors make only five; but Huxley, in perfect consistency with a plan which is in itself defective, makes six). These are: 1, the *rhinencephalon* (olfactory lobes and bulbs); 2, the *prosencephalon proper* (hemispheres); 3, the *thalamencephalon;* 4, the *mesencephalon;* 5, the *metencephalon* (cerebellum); and 6, the *myelencephalon.* The first three are produced from the fore-brain, the last two from the hind-brain. We do not accept this classification, first, because it has proven the chief hinderance to homologizing the brains of the lowest vertebrates (as witness the Stieda, Michlucho-Maclay and Gegenbaûr controversy); then also because the corpus striatum should be raised to as distinct a position as the thalamus; and, finally, because the cerebellum originates as a local hypertrophy, *not a distinct segment* of the medulla oblongata. We hence admit only three cerebral vesicles.

§ 42. Although from our point of view the thalamus is in parallelism with the corpus striatum, in so far as they are both developed from the same cerebral sub-vesicle with, and are both dependencies of the cerebral hemispheres, there are certain differences. Just as the thalamus was situated between the balance of the prosencephalon and the mesencephalon, it shares characteristics of the hemispheric ganglia on the one hand, and the automatic ganglia on the other. It is physiologically as it is anatomically a connecting link between the cerebrum and the medulla oblongata.

In animals whose cerebral hemispheres are poorly developed, and where on account of the defective character of fibres which pass directly to the corpus striatum and cortex, the relations of those fibres which enter the thalamus from below are best studied, it can be seen that the strands which pass through and around the reticular ganglion enter the thalamus and even connect with its cells. Lesions of the thalamus are known to produce certain abnormalities of position, distortions of the bodily axis, and consequent disturbance of locomotion; for this we have the following anatomical basis:

The strands which enter the thalamus can be traced both from the lateral and posterior columns of the cord. More fibres enter it from below than connect it with the rest of the hemisphere (by emerging above), hence some of these strands

must terminate in the thalamus without directly connecting with the hemispheres or corpus striatum. On the other hand anatomical research renders it highly probable that *some* of the strands connecting the cord and thalamus are interrupted by the cells of the reticular ganglion. We have thus an intricate arrangement of the ganglia and fibres which we represent in the annexed diagram.



The thalamus rises to the rank of a ganglionic category higher by one in the scale than the reticular ganglion. It is a representative of the *third category* and the thalamic fibres represent tertiary projecting tracts.

How the position of the thalamus as an independent centre is encroached on in the highest animals and how its relations are complicated in man, will be discussed in the limits of this chapter: the manner in which the fibres terminate and connect, in the chapters following. For the present we will content ourselves with pointing to the fact that when we speak of certain fasciculi being interrupted by cells of the reticular formation (reticular ganglion) we do not mean to say that the same fibres connected with thalamic cells can be identified as the ones connected with the cells in the reticular ganglion, but that the fibres of the *same fasciculus* are seen to be so connected. From this we draw the above inference. Meynert has named the thalamic fibres "motorisches Feld" of the human isthmus, and speaks of the

cells of the reticular field (which we have named reticular ganglion in their aggregate) as scattered depots of the cranial nerve nuclei, agreeing in this respect with Deiters. True it is that on the one hand these cells do connect with the nerve nuclei, but we have offered another explanation for this relation (§ 37), one which does not fail as Deiters'-Meynert's explanation fails to cover that voluminous accumulation, known as "Kern des Seitenstrangs" (nucleus funiculus lateralis).

§ 43. Since the thalamic fibres, whether interrupted by the scattered cells of the isthmus or not, can be traced into both the lateral and posterior columns of the cord, it follows that the thalamic cells must be mediators between sensory impressions originating in the trunk and extremities and the movements which are determined in these parts. At the same time we remark that this ganglion in higher animals is not a mere homogeneous aggregation of nerve cells, but that these cells are arranged in definite groups (Fig. 7), which show considerable variation in the animal range and are separated by transmigrating fibres which enter, are lost in or connect with these different accumulations. This anatomical complexity seems to be the expression of a co-ordinating faculty. Anatomically it would be hazardous to infer such a faculty from the mere structure, but physiologically and pathologically the anatomical inference becomes entitled to consideration as at least a very reasonable theory (seq.)

§ 44. The portion of fore-brain anterior to the thalamus, undergoes a subdivision into the two cerebral hemispheres. These are in the urodelous amphibians of a remarkably simple structure. The cells are congregated around the ventricular cavities, just as those of the cord are in all animals in relation to the lining of the central canal. In man and higher animals the grey matter, with one local exception to be alluded to, is separated from the ventricle by the massive development of white substance, but in the embryo the white substance being absent, we have the same relation as in the urodela. Therefore the hemispheres are originally a part of the central tubular grey matter, and the same transitions between the epithelia lining the ventricle and the cells of the cortex can be traced, as were referred to in the case of the cord and medulla oblongata (§ 26).

In simpler forms, the entire thickness of the hemisphere is

ganglionic substance (Fig. 5), in higher ones, white substance is developed, but not as in the cord on the outside of the ganglionic matter, but on its *inner aspect, the conducting fibrils separating the future cortical nerve cells from the epithelium* lining the ventricles (Fig. 6.) As we progress upward in the scale we observe that both the thickness of the white substance and especially of the grey substance undergo an enormous increase.

As the existence of a ganglionic depot without associating or projecting connections would be nothing less than an absurd assumption, it is to be concluded that in the animals possessing cortical without medullary substance, the conducting substance is fibrillar. This we have found actually to be the case, and the more searching inquiries of Schmidt ("Structure of Ganglionic bodies," *Journal of Nervous and Mental Disease*, 1879), have confirmed for the *amphiuma* what we have found in the *menobranchus*. That in the simplest forms, the ventricular epithelia may themselves be of a nervous nature we consider highly probable. Fibrillæ which are unquestionably nervous I have traced among and around the epithelial nuclei, in the true reptiles as well as in the amphibia. Schmidt (*loc. cit.*) has done the same, and Rohon (*Das Selachiergehirn*, Denkschriften der Kaiserlich. Akad., 77), remarks the great similarity of certain epithelia from the fourth ventricle to the epithelia of the peripheral sense organs. In this regard it deserves mention that one of the great masters of cerebral anatomy, Stilling, to his dying day, held all the epithelia surrounding the central canal of the cord to be of a nervous nature. While we should conclude from their relative atrophy in the human being that their nervous functions had become unimportant and perhaps entirely supplanted by secondarily developed and specialized ganglia, yet we would accord weight to the statement of Stilling as establishing a widespread homology of the nervous epithelia.

While there is a marked contrast between the hemispheres and cord (as stated in the text) with reference to the development of the white substance, it should be stated that certain convolutions, particularly those related to the olfactory lobe, develop white substance on the *outside* as well as on the inside of the grey matter. These gyri are the oldest genetically, and atrophy in man, showing that their functional importance is less in the latter. In the accompanying three figures a black space on the outer side of the cellular layer represents molecular substance belonging to the cortex proper; it is like all the molecular substances, relatively most massive in lower animals, and already the lower mammalia (Fig. 6) show less of it than the reptiles.

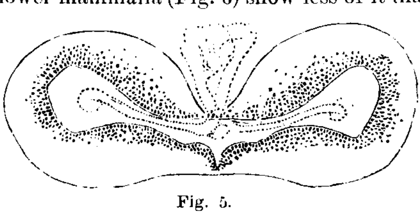


Fig. 5.

Transverse section of hemispheres, from American proteus (*menobranchus lateralis*). The dotted contour represents the tela choroidea, detaching the choroid plexus into the here common ventricular cavity through the atrophied prosencephalic roof or lamina terminalis.

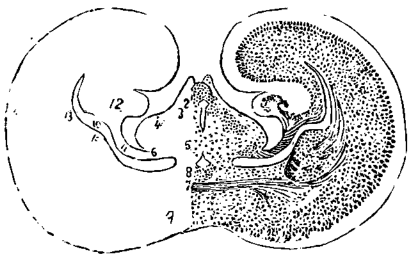


Fig. 6.

Same from small European bat (*vesperugo noctula?*): (x) barren layer of cortex; (12) cornu ammonis; (8) undifferentiated basilar grey; (9) cortex continuous with same; (13) white substance (corona radiata); (14) corpus striatum; (7) olfactory decussation (commissura ant.); (10) lateral ventricles; (12) cornu ammonis; (2, 3, 4, 5, 6) nuclei of thalamus; (6) for termination of fornix (11).

§ 45. We stated (§ 44) that with one local exception, all the grey matter of the hemispheres became separated from the ventricles and their lining by the developing white substance. The exception in question is at the floor of the ventricle, where the white fibres, swerving from their course, cut into the grey substance in such a way as to leave one portion in contact with the ventricular lining, *the corpus striatum*, driving the other part out, as they did the rest of the cortex (Fig. 6).

Before this differentiation occurred, the anterior portion of the hemispheres developed a distinct appendage, containing a prolongation of the lateral ventricles, and termed, from its relations to the *regio olfactoria*, the *olfactory lobe*. This olfactory lobe and the corpus striatum are in direct continuity, and manifest intimate relations throughout the animal range.

Evidently the sense of smell is one of the most important in lower animals. However much this sense may have lost in importance in the human species, which makes up for the deficiency in countless other ways, and in birds, whose acuteness of vision vicarates for the almost complete absence of this sense, yet in all water breathers it is one of the conditions of their existence. Even in land animals, not only in the car-

nivorous, but also in the herbivorous species a great portion of the psychical life is based on olfactory conceptions.

Now water breathers constituted the ancestry of the vertebrate sub-kingdom, and it is reasonable to suppose that the olfactory lobe constitutes one of the most ancient differentiated segments of the central nervous system. In the myxinoid fishes and the lamprey *the* CEREBRAL HEMISPHERES THEMSELVES *are mere appendages of the olfactory lobes, and hardly half their size.*

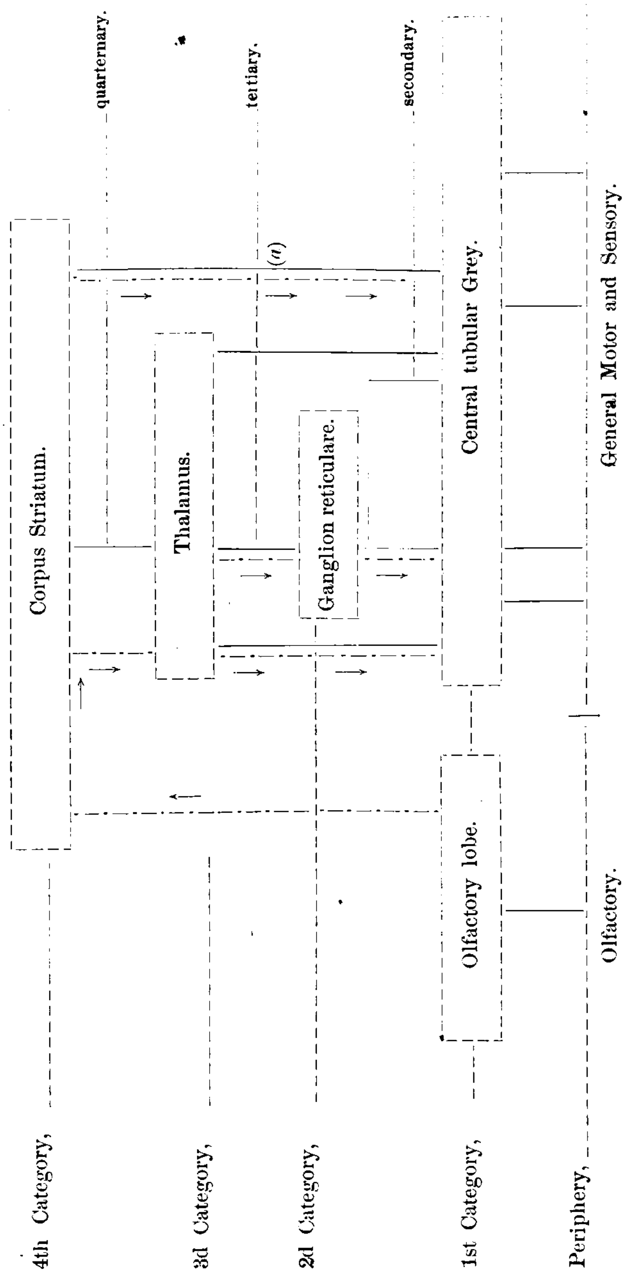
This fundamental importance of the olfactory lobe implied a corresponding development of the associating conductors, which bring the impressions of this sense into such relations with *the motor* apparatus, as to permit of their utilization for the purposes of the animal economy.

These conductors could travel but in one way, namely, through the corpus striatum and the thalamus or sub-thalamic region, after passing the corpus striatum. This is in lower animals; in higher, more complicated relations are established.

Now the olfactory lobe clearly represents a first category of grey matter, for its periphery is projected in it directly by the filamenta olfactoria without the intervention of any intermediate ganglia.

But the corpus striatum, superior to the thalamus in position, and receiving fibres which have passed through the latter, is equivalent to a fourth category of grey matter, as we will establish more fully.

Since the fibres of the secondary projection from the olfactory lobe connect with the corpus striatum, we have a secondary projecting tract terminating in a ganglion of the fourth category. This is one feature which gives the olfactory nerve a high position in the scale of the cranial nerves—one, in fact, which establishes a profound difference between it and other cranial or spinal nerves, except one—the optic—which we shall find to merit an equally special position.


quarternary.
tertiary.
secondary.
(a)
Corpus Striatum.
Thalamus.
Ganglion reticulare.
Central tubular Grey.
General Motor and Sensory.
Olfactory lobe.
Olfactory.
4th Category,
3d Category,
2d Category,
1st Category,
Periphery,

In this diagram the broken and dotted line with the arrow represents the path taken by a sensory impression, traveling to the olfactory lobes, thence transmitted to the motor ganglion, and down through the peduncular axis to the motor periphery. The multiplicity of paths emerging from the corpus striatum is introduced to represent the *anatomically* various *possible* tracks which any motor impulse may travel. Of their conditions of development more anon; but in passing, we may indicate that the very existence of both direct and more or less interrupted fasciculi connected with the same category of grey matter, shows that a *strict classification of the projecting fibres into primary, secondary, tertiary, etc., cannot be practically carried out.* We employ such a classification merely as a provisional and theoretical one, in order to systematize somewhat the intricate tracts which connect the different ganglia with the more or less remote periphery, and to furnish a basis for a subsequent physiological speculation. The same applies to the ganglionic "categories."

§ 46. Not quite as early in its appearance, and not as pronounced in physiological importance (in the lowest vertebrates) we have the visual periphery developed. In the higher vertebrates so prominent does this sense become, and so intimate its relations to the psychical life, that, *ab initio*, the embryonic trace of the retina is developed in *direct continuity with the nervous axis.* Originally connected with the central tubular grey matter of the third ventricle, it secondarily develops a projection in the *dorsal part of the second* cerebral vesicle—the mesencephalon. Its primary projection loses in importance and becomes an atrophic remnant in man, probably as devoid of function as it is devoid of any special structure and connections. This is Meynert's *basal optic ganglion.*

§ 47. In entering the mesencephalon, the optic nerve spreads out on the surface of this vesicle. At the same time there is developed within the ganglion other conducting substance, which separates the outer cells from the inner.

The inner cells retain the position and the signification of a central tubular grey; the outer cells constitute the *essential ganglion of the optic lobes*, and exhibit a *cortical* structure. This fact is of some significance. The cortical structure is one

which is employed wherever a given periphery is to be accurately and exhaustively projected. It is manifested in the olfactory and optic lobes in the cerebum and cerebellum.

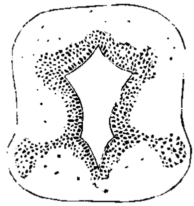


Fig. 7. Optic lobe of menobranchus.

§ 48. Thus, while the optic lobes of the lowest animals (Fig. 8) show merely the central tubular grey, in higher ones we find, 1st, the superficial white substance constituting a primary projection path, and derived from the optic tract; 2d, a grey ganglionic layer, the *primary centre of vision;** 3d, a deep, white layer; and 4th, the central tubular grey.

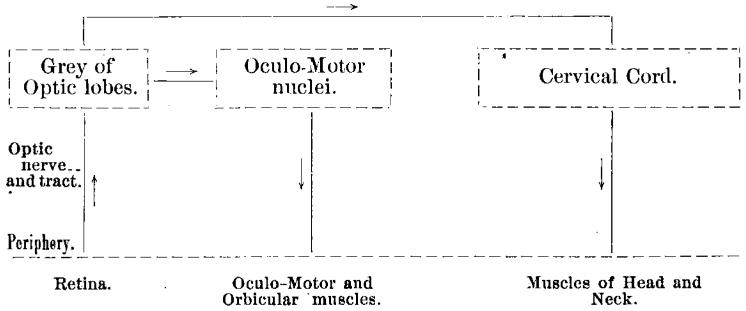
The deep white matter connects the visual centre with the oculo-motor nuclei in the first place, and with undetermined nuclei of the spinal cord in the second. As the fasciculus which establishes this latter association gradually becomes exhausted in the cervical region, and maintains its anatomical continuity as a fasciculus only by receiving fresh accessions of fibres from other sources, we may assume it to terminate in the nuclei which control the reflex movements of the head and neck.

The optic nerves and tracts constitute a primary projection tract; the cortical grey of the optic lobes a first ganglionic category; the deep white substance is an associating tract of the lowest or first order, connecting two ganglionic stations of the first category.

Omitting the already assumed projecting systems, we may represent the above relations in the subjoined plan:

* In a physiological, but not in a phyllogenetic sense.

1st Category.



Although we have here ranged the optic lobes in the first category, it is seen from the above diagram that they extend their sway over a considerable motor territory, and like the olfactory lobes occupy a special position, in contrast with the other cranial nerves.

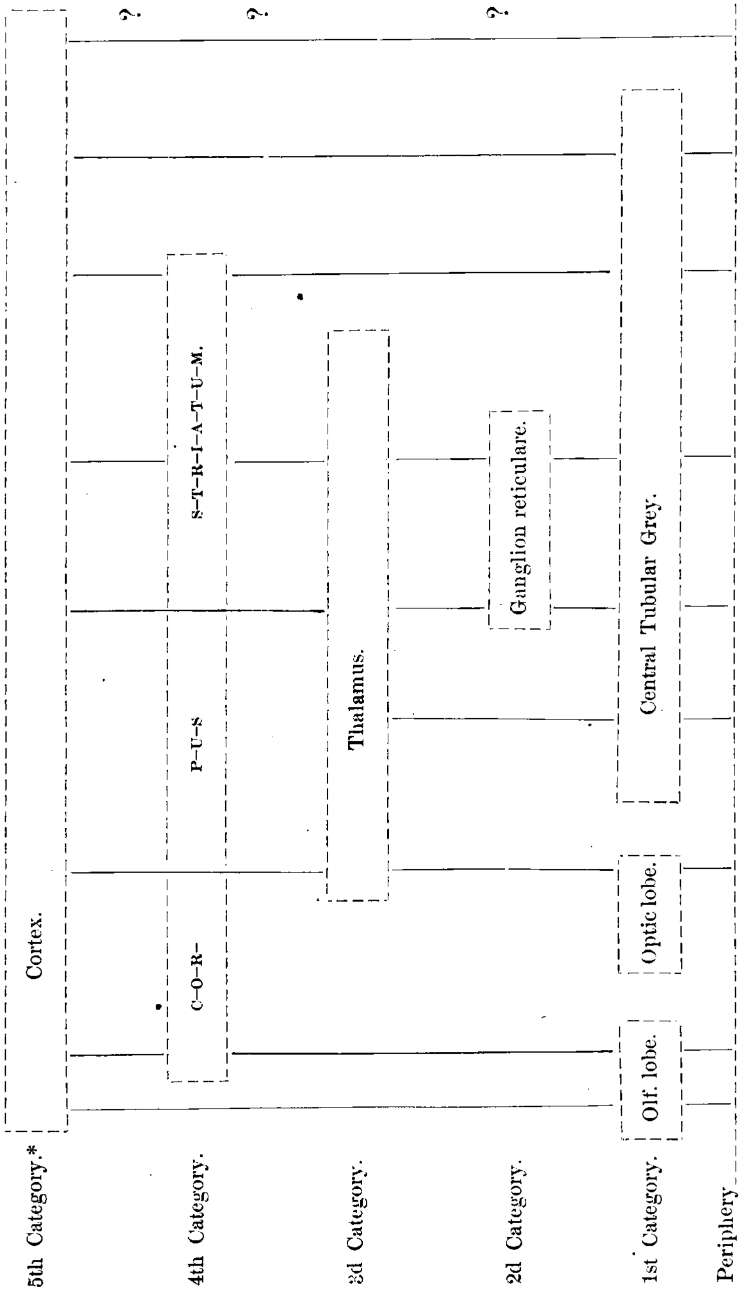
§ 49. We have now traced (theoretically for the present) the anatomical basis of certain co-ordinations; co-ordinations which were based on associations between the sensory and motor peripheries, and which according as they involved a lower or higher category of grey matter were more or less limited in their range of complexity. The first projection systems simulated so many simple mirrors, each of which reflected a portion of the object presented to the series, while the second and higher systems simulated larger mirrors which collected by re-reflection the sum of the images projected on the smaller mirrors, and combined them into pictorial unities. But as yet there were still several unities: the optic lobes representing one; the olfactory and corpus striatum another; the thalamus and its dependencies a third. To unite them in function, mutual associations became necessary, and these thenceforth join in anatomical embrace all the great basi-cerebral ganglia. This *association is the basis of the highest so-called automatisms.*

§ 50. It is almost a rule in morphology that where several structures co-exist in functional union, one or the other will preponderate, and the higher the structural union becomes developed, the more decidedly does the superiority of the predominating member become marked.

The olfactory lobe bore such important relations to the life-history of early vertebrates, that we are not surprised to find the *cerebral hemispheres* developing at first as mere appendages of the olfactory lobes (§ 45).

The corpus striatum representing a fourth category of the projection grey, projected in turn its innervations in the hemispheric grey, thus constituting the latter a *fifth order*. Then the thalamus found besides the indirect projection through the corpus striatum already referred to (§ 45) a direct connection with the cortex. The optic lobes followed, first by indirect projection through the thalamus, then by a special circuit, through the ganglion geniculatum externum (seq.).

With the development of these highest projection fibres the cerebral hemispheres gradually encroached on the independency of the lower ganglia, until in its maximal development as found in man, it resembles a great empire which holds a number of tributary states in sway under a common powerful rule. The anatomical unity now attained, finds its parallel psychical culmination in that more perfect consciousness of the *ego* which is peculiar to man.



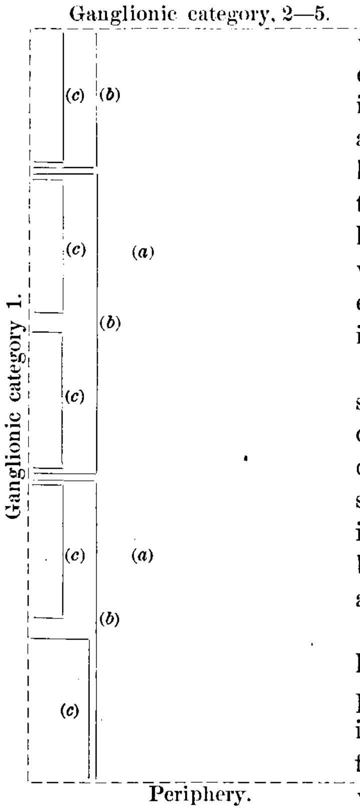
*It will be hardly necessary to remark that topographical representations are not even remotely aimed at in these diagrams.

§ 51. In this preliminary sketch, it being purely our object to formulate the principles of the cerebral architecture, we shall not find it necessary to discuss the relations of the cerebellum, or of the intercalar ganglia. We would be merely repeating the same theorems and deducing the same laws as those we are now preparing to make a summary of.

All through these last paragraphs we have found one striking feature in the elaboration of the projecting tracts, namely that, in higher developments, the fasciculi show a tendency to emancipate themselves from the interruptions offered by intermediate ganglionic categories, in short that the tendency is, to establish a direct communication between the cortex and the central tubular grey matter. It is the same tendency which led to the development of the longitudinal tracts of the cord, thus establishing a readier association than the circuitous route furnished by the fibrillary net-work of the grey substance.

The course of this development is determined by two physiological laws: the first is, that, the greater the distance traversed, the longer will the impression take to travel to its destination; the second is, that every ganglionic element to be traversed delays the transmission of the nerve current.

In the diagram, the conducting path (*a*) is far more perfect as a mechanism than (*b*), and (*b*) is in its turn more perfect than (*c*).



§ 52. While the first law if it were the only one which governed the conducting mechanism, would tend to produce an atrophy of the intercalar ganglia, the second, which up to a certain point has the same tendency, has a conservative element in it, which operates against such an entire abolition of the interrupting stations.

It is desirable for certain physiological purposes, that the mechanism by which nerve currents can be arrested at certain points, should be maintained. Many inhibitions doubtless take place by virtue of this interrupting arrangement.

§ 53. In order that all physiological necessities may be complied with, we must assume that in man, the projecting system falls into two groups: the one which shows a tendency to emancipate itself entirely from the interrupting ganglia, the other which maintains its connections with the latter. The continuous tract of the internal capsule, pes pedunculi, vertical pons fibres, anterior pyramids, and part of the lateral columns of the cord, is an example of the most direct variety. The posterior part of the corona radiata, the thalamus, thalamic fibres, reticular ganglion, other portions of the lateral columns, represent a form of the indirect variety. Both are necessary to the purposes of the organism, but the indirect variety being devoted to the organic needs, and these needs being the same in all animals, or nearly so, shows less variation in the zoological range than the direct. The latter which typifies the domination of the intellectual centres rises in a mathematical ratio as we approach the human being. So that

in man, while the *automatic ganglia and tracts remain about the same in mass as in the other mammalia, the intellectual ganglia rise far above them, and this gives rise to the apparent but not real diminution of the automatic systems observed in the human brain.*

§ 54. Certain actions which, while the hemispheres and higher ganglia were yet poorly developed, were presided over by the central tubular grey, or its immediate derivatives, become translated *bodily* to higher systems in higher animals. This accounts for the atrophy of finally useless centres which persist only in accord with the uniform plan of development manifested in any group of animals. Thus the optic lobes, though extremely rudimentary in blind genera, still are present. The basal optic ganglion (§ 46) is another example of the persistence of the supplanted and physiologically defunct centres; the grey of the locus perforatus, and the interpeduncular ganglion hold similar positions.

Thus far we have traced cursorily, because for merely provisional purposes, the general plan of the cerebral architecture. We have seen that the entire central nervous axis was a development from the central tubular grey, a portion of which retained its primitive position in the shape of the first ganglionic category.

This *axial* grey matter is genetically the earliest, anatomically the easiest studied, and physiologically the simplest of all the ganglionic systems; and just as structurally it was the primordial fundament from which all the higher ganglia became gradually elaborated, so functionally it is the basis on which they rest.

Our description of the Architecture and Mechanism of the Human Brain will, therefore, begin with the discussion of the axial ganglia, more familiarly known as the cranial nerve nuclei proper, and of their connections.

(*To be continued.*)